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SUBALPINE LAKE-SHORE VEGETATION IN NORTH-CENTRAL COLORADO

FRANCIS RAMALEY

INTRODUCTION

Very little has been published on the shore vegetation of lakes in Colorado. Brief references were made to lakes of the Pike's Peak region a number of years ago by Clements (1, 2). A somewhat extended account by the writer and W. W. Robbins (9) described the associations at Redrock Lake, Boulder County, Colorado, in the subalpine zone. Later, a short paper (5) pointed out certain features of shore vegetation in the montane zone. Recently Dr. Robbins has given a most careful and illuminating description (11) of a number of lakes in the montane zone near Tolland, Colorado. The present writer, dealing with sedges of northern Colorado, has named and characterized (7) certain of the plant associations of lake shores at different altitudes. In a paper by Dodds (3) on the plankton crustacea of Colorado lakes there are some references to vegetation and a very good account of physiography and climate.

The following pages give the results of a study of subalpine lakes, the study carried on chiefly from the University of Colorado Mountain Laboratory (8) at Tolland, Colorado, during the last ten years. A later paper will take up alpine lakes.

PHYSIOGRAPHY

The area in which lake-shore vegetation has been studied is a strip about 5 miles wide, along the eastern slope of the continental divide and extending from the southern boundary of the Rocky Mountain National Park south to Parry Peak, a distance of 24 miles. About 50 of the subalpine and alpine lakes of this district have been visited, and also a few on the western slope, in Grand County (see maps, figs. 1 and 2). The subalpine lakes more carefully studied are listed below together with altitudes in feet above sea level. These lakes are all of small size, the largest scarcely more than a half mile in length.

Lakes in Boulder County: Redrock Lake (10,100), Brainard Lake (10,350), Long Lake (10,500), Silver Lake (10,200), Emerald Lake (11,250), Dixie, or Jenny, Lake (11,000).

Lakes in Grand County: Corona Lake (11,165), Corona Reservoir (11,350), Lake Epworth (11,250).

Lakes in Gilpin County: Forest Lakes (10,800–10,900), Arapahoe Lakes (10,700–11,200), Crater Lakes (10,400–11,000), Echo Lake (11,072), James Peak Lake (11,090).

Lakes in Clear Creek County: Steuart Lake (11,350), Reynold's Lake (11,350), Loch Lomond (11,140).

The continental divide in the area studied is, for the most part, about 12,000 feet above sea level, with a few passes slightly lower and certain peaks much higher (Mt. Audubon, 13,225; Arapahoe Peak, 13,506; James Peak, 13,260; Parry Peak, 13,345). Long ridges extend out peninsula-like from the divide. Between the ridges are deep valleys all or most of which held glaciers at various points during comparatively recent times. On Arapahoe Peak there is still a permanent glacier of considerable size. A mile to the north is a smaller one (Henderson Glacier) and two others, also small, the Fair Glacier and the Isabelle Glacier, are four miles farther. At the extreme northern limit of our area of study are two more, the St. Vrain Glaciers. The broader parts of valleys are from one half to three quarters of a mile in width, and each may hold a group of small lakes, sometimes six or more. Along the flanks of ridges and on the slopes of the divide there are numerous cirques each with a single small lake.

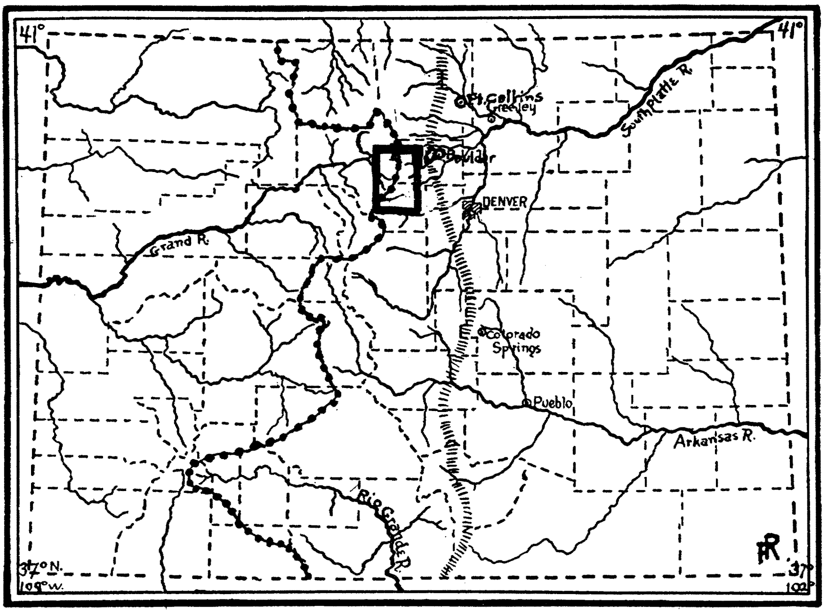

FIG. 1. Key map of Colorado. The Continental Divide is shown by the heavy dotted line, the front range of foothills by the short horizontal lines. The black rectangle outlines the area in which lake vegetation has been studied. Immediately north of this area is situated the Rocky Mountain National Park (not indicated on the map), of about the same size and shape as the part here marked out.

The higher lakes are chiefly of the rock-basin type while those of the subalpine zone are usually morainal. No ox-bow lakes are known to the writer above 10,000 feet altitude, although they occur in parks of the montane zone (8,500 to 10,000 feet).

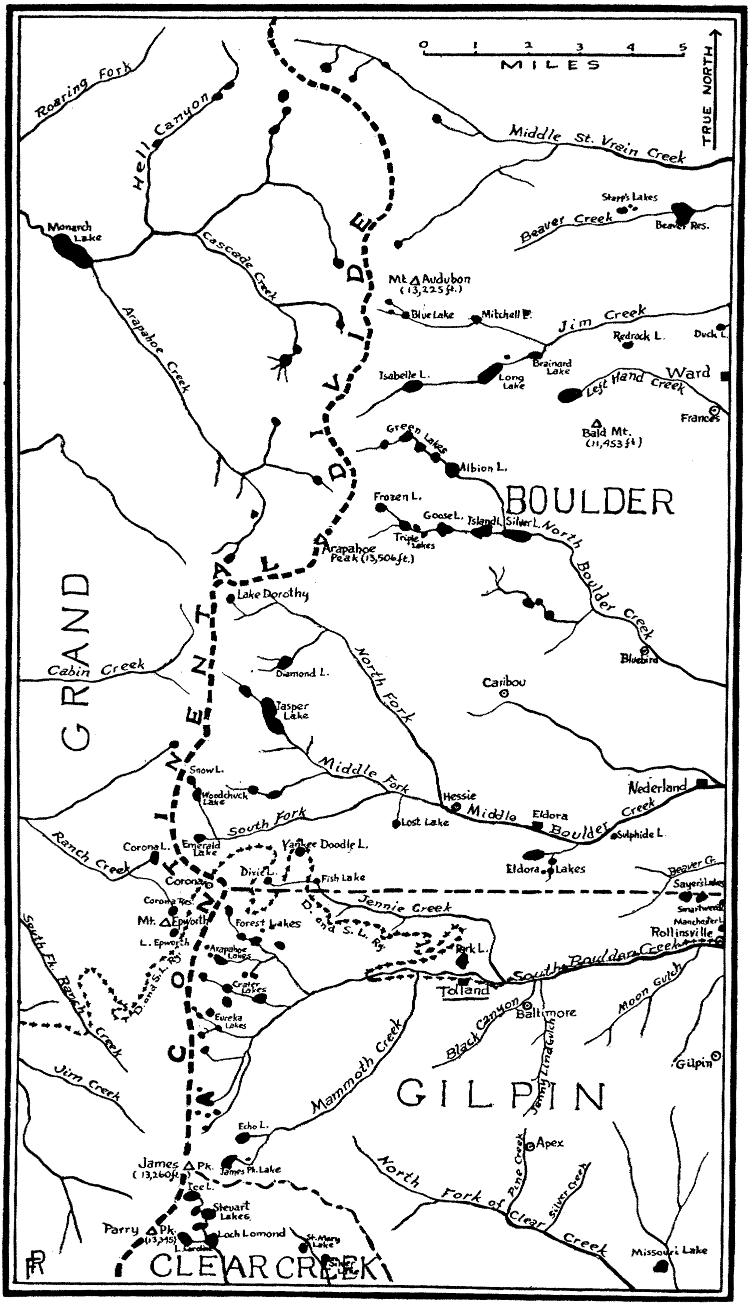

FIG. 2. Map of the area in which lake vegetation has been studied, *i.e.*, the part of the state included in the black rectangle of figure 1: portions of Grand, Boulder, Gilpin, and Clear Creek counties. The Continental Divide is in most places about 12,000 feet in altitude. Lakes close to the divide are of the alpine type; those from one to four miles away, and hence at lower altitudes, are generally of the subalpine type. The University of Colorado Mountain Laboratory located at Tolland, in Gilpin County, has served as the usual base from which trips were made on foot, but Ward, in Boulder County, was used as headquarters for the study of Redrock Lake.

Climate and Soil

The climate of the area under consideration is cold, corresponding to that of Labrador, the Hudson Bay country, and southern Greenland. The timber limit is about 11,500 feet; lakes above this datum I shall speak of as alpine, those between this altitude and that of 10,000 feet as subalpine.

At Corona, on Rollins Pass, at an altitude of 11,660 feet, a government weather-bureau station was maintained (3) for a number of years. Here the mean annual temperature was found to be 26 degrees F. and the precipitation 43.7 inches. These figures may be taken as representative of the alpine region in this part of Colorado, although the tops of the higher peaks are, no doubt, colder and wetter. Throughout the alpine district there is frost every month of the year and in many places nearly every day.

For the subalpine zone only very incomplete records are available, but it is likely that at 10,000 feet the mean annual temperature is about 36 degrees F. and the precipitation 30 inches. The period without frost does not exceed three or four weeks even in favorable seasons. Precipitation is always ample during the growing period. There are frequent light showers during July and August (8). In table 1 a comparison is made with various points in the northern United States so that a clearer idea of the climate of our area of study may be gained.

TABLE 1. *Temperature and precipitation in the subalpine and alpine zones of Colorado compared with data from various points in the northern United States. Temperature in degrees Fahrenheit; precipitation in inches*

Station	Mean Annual Temperature	Mean July Temperature	Mean Annual Precipitation
Subalpine zone (10,500 ft.)	34.0[1]	54.0[1]	32.0[1]
Alpine zone (Corona, 11,660 ft.)	26.0	47.0	44.0
Denver, Colo. (5,275 ft.)	49.8	71.8	14.0
St. Paul, Minn.	45.0	74.0	28.6
Duluth, Minn.	39.0	66.0	29.9
Chicago, Ill.	48.0	72.0	33.4
New York, N. Y.	52.0	74.0	44.8

The temperature of the soil, as would be expected, is low. Numerous observations have been made at subalpine lakes. Readings at 3 dm. depth are shown in table 2. In analogous associations at ordinary altitudes in the northern United States the temperatures are 10 to 18 degrees higher.

TABLE 2. *Soil temperatures of subalpine lake shores for July; average of numerous observations at 3 dm. depth, in degrees F.*

Subalpine sedge moor, near water	50
Subalpine meadow, on higher ground	52
Subalpine spruce forest (dense)	48
Subalpine forest openings (dry places)	60

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[1] Data very meager; estimated by comparison with stations in the alpine and montane zones.

Soils throughout the area studied are derived primarily from granitic rocks. On many ridges the material is a compact disintegrated granite, and the shores of subalpine lakes are often of this material interspersed with large and small boulders. At inlets and outlets, and wherever an accumulation of wash from adjacent slopes occurs, the soil is a black loam. Here sedge moor and willow moor (willow scrub) develop. Typical subalpine meadow is found on lighter, better-drained soil, a sandy loam which occurs often as a circum-area of lakes between the moor and the forest.

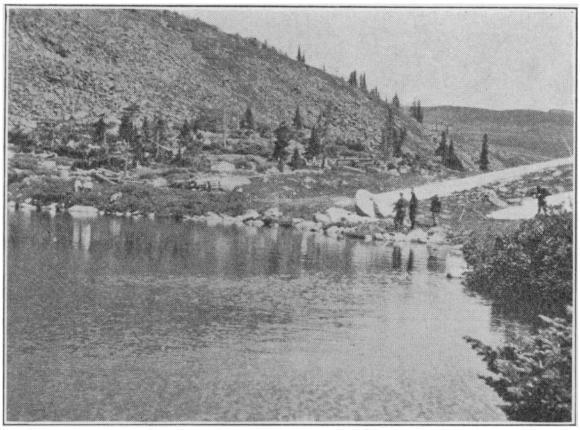

FIG. 3. Part of Corona Lake (altitude 11,165 feet), a high subalpine lake without any complete circum-areas of vegetation. Numerous large rocks are to be noted along the shore which show that there has been very little infilling. In the lower right-hand corner of the picture an Engelmann spruce is seen; behind this is a clump of willows; farther around is sedge moor; then more willows.

Soil moistures have not been so fully determined as soil temperatures. Figures for July, 1918, at Redrock Lake (altitude 10,100 feet) are, however, available (9). They indicate an abundance of moisture. Averages are shown in table 3.

TABLE 3. *Soil moisture percent at 3 dm. depth during July, 1908, at Redrock Lake in the subalpine zone*

Subalpine sedge moor, near water	65
Subalpine meadow, on higher ground	21
Subalpine spruce forest (dense)	29
Subalpine forest openings (dry places)	7

No studies of wilting coefficients have been made, but so far as the writer's observations go there is little wilting of vegetation even in the driest weather.

Probably the chief limiting factors for plant growth around subalpine lakes are low temperature, extreme shortness of season, and shallow soil.

At very high altitudes there can be no doubt that the drying effect of winter winds and the heavy snows are important in preventing forest development.

PLANT COMMUNITIES OF LAKE SHORES

Types of Zonation

Great similarity exists in the shore vegetation of the various lakes studied. It is convenient, as already suggested, to separate subalpine and alpine life-zones by an arbitrary datum of 11,500 feet altitude. There is, however, no sharp difference in vegetation immediately below and above this line, yet it is possible to distinguish a subalpine and an alpine type of lake. The former only will be considered in the present paper. So far as the writer is able to do so, he will use a terminology consonant with that proposed by Nichols (4). Plant nomenclature will be that of Rydberg (12).

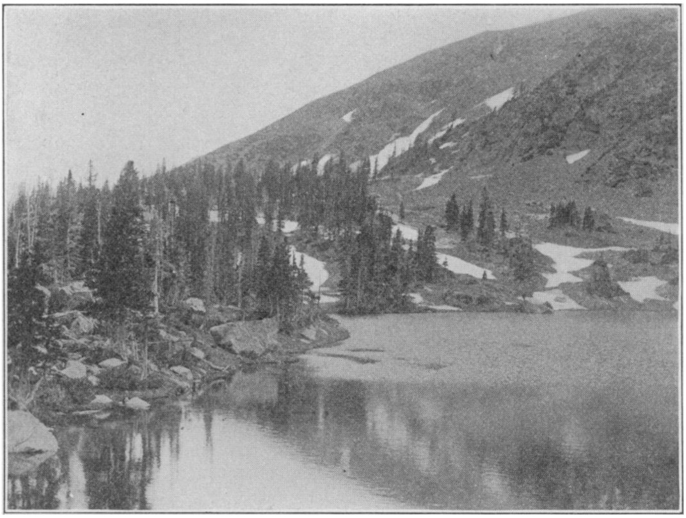

FIG. 4. One of the larger Forest Lakes (altitude 10,800 feet), showing coniferous orest of Engelmann spruce coming down close to the lake edge. There has been very little infilling either through wash from the slopes or through accumulation of plant remains. At the left there is a narrow fringe of moss moor; on the shore opposite the observer a considerable amount of meadow moor has developed in the lower places close to shore. Photograph in early June by Dr. W. W. Robbins.

Subalpine lakes are typically surrounded by Engelmann spruce forest in which subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus murrayana*) may occur in small amount. Aspens (*Populus tremuloides*) are occasionally present, but they belong rather to the montane zone where they are very abundant. On the eastern wind-swept shores of lakes the forest is often made up largely of limber pines (*Apinus flexilis*), the trees scattered with intervening open spaces.

Lakes shut in by steep slopes often show no special shore vegetation. The Engelmann spruce forest extends down close to the lake edge, and here there may be a zone of rocks with almost no vegetation at all. This condition obtains particularly where the lake level fluctuates from year to year or in different months of the same season. Most lakes have some parts of the shore either barren or else covered with forest. Lakes which show no true shore vegetation furnish nothing for discussion in the present paper.

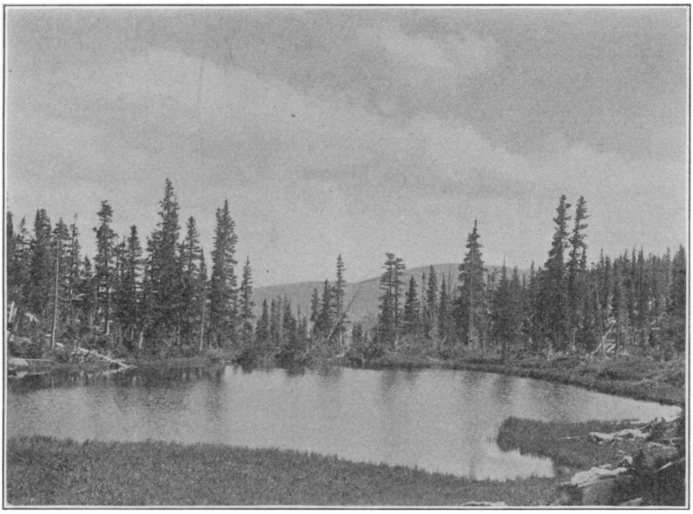

FIG. 5. One of the small Forest Lakes (altitude 10,800 feet); a shallow pond with much infilling and showing complete circum-areas of moss moor and sedge moor. A half submersed belt of *Carex aquatilis* runs about one third of the way around the lake. Nearly every one of the various lake-shore associations is represented in some part of the area surrounding this lake. Photograph by Dr. W. W. Robbins.

Many lakes have gently sloping banks for a part of their circumference. On these more moderate slopes a true shore vegetation develops, determined by differences from the forest in soil quality, soil moisture, and soil temperature. A common arrangement of the vegetation of these lakes is in three clearly-marked circum-areas (8). As a rule, some of the associations are absent at certain points. Willows may be present only near the lake inlet and outlet (see table 4).

TABLE 4. *Subalpine shore vegetation; condensed classification*

1. Moor; next to water:
    - *a.* Sedge moor; chiefly Carex, with Caltha, Bistorta, Clementsia, and other marsh plants.
    - *b.* Willow moor (willow scrub); farther from the water but the soil very wet. The herbaceous vegetation is chiefly Carex with some shade-enduring grasses and dicotyledons.
2. Meadow; on drier ground, but the soil fairly deep and of moderately fine texture. Often this is a close association of many species of flowering herbs.
3. Forest; Engelmann spruces chiefly, if the soil is deep, but lodgepole pine and limber pine on steeper slopes and on ridges with scanty soil.

In favorable parts of subalpine lake shores a closer analysis of the vegetation can be made than is indicated in table 4. Thus the moor is seen to include as many as six communities arranged in successive belts; a heath association may be distinguished outside the moor, *i.e.*, in drier ground; two or more consociations may form distinct bands in the meadow association. All of these communities are associated with differences in edaphic conditions and are not merely floristic in nature. Such a vegetation complex is indicated in table 5.

TABLE 5. *Subalpine shore vegetation, extended classification*

1. Moor (moor-association type):
    - *a.* Half submersed association of *Carex aquatilis.*
    - *b.* Moss-moor consociation; sedge moor with large amount of moss.
    - *c.* Typical sedge-moor association.
    - *d.* Willow-moor association; sedge moor with shrubby willows.
    - *e.* Rush-moor society; sedge moor with rushes (*Juncus Drummondii* and *Juncus mertensianus*).
    - *f.* Meadow-moor consociation; sedge moor with a number of meadow plants and hence a smaller proportion of Carex than typical sedge moor.
2. Heath association:
    - *a.* Heath moor, a transition between heath and moor.
    - *b.* Kalmia heath consociation.
    - *c.* Gaultheria heath consociation.
3. Meadow association:
    - *a.* Erigeron-Castilleja-Ligusticum consociation.
    - *b.* Pedicularis-Vaccinium consociation.
4. Forest association.

It seldom occurs that all these communities can be distinguished for any great distance along the shore. Many lakes have a part of the shore in which the vegetation analysis may be carried as far as indicated in our table, other parts of the shore may show no more than is suggested in table 4, while still other parts have no distinct shore vegetation at all. An abnormal position of some of the communities is often brought about, due to local areas of seepage. Islands of meadow moor occur in many places surrounded by sedge moor, while similar islands of willow moor and moss moor are common (see map, fig. 6). Meadow moor, rush moor, and the entire heath association are absent from many lakes. The positions of heath and meadow are sometimes completely reversed, or there may be heath meadow in which there is a mingling of plants of the two associations. Lakes near to timber limit may have little vegetation except meadow moor, or sedge moor and meadow moor.

Descriptions of the Various Lake-shore Zones (Circum-areas)

The *half submersed Carex aquatilis association* is typically a pure stand of the species of Carex which gives its name. This is in contrast to conditions in montane lakes (5, 7, 11), where three or more species may make up the half submersed zone.

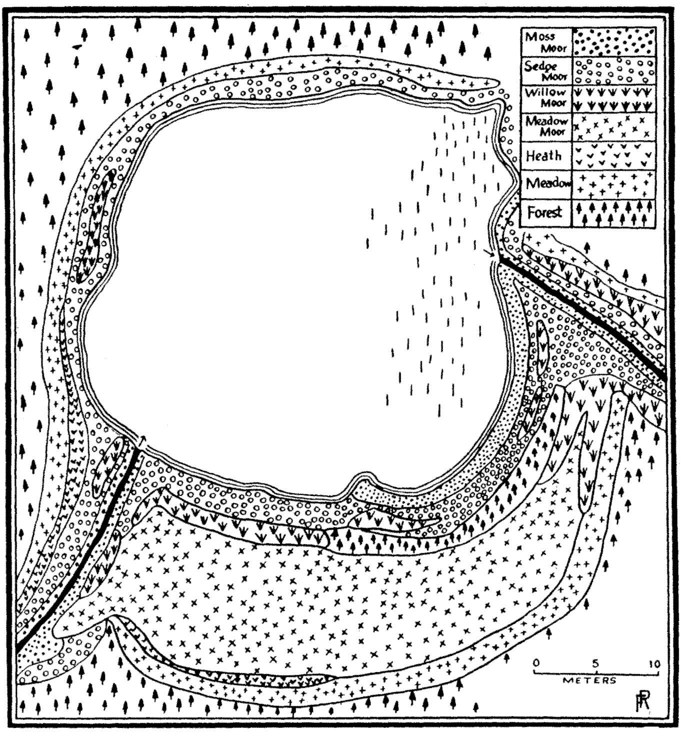

FIG. 6. Map of vegetation at Burgrass Lake, one of the Forest Lakes, a small subalpine pond at an altitude of 10,800 feet. Scattered plants of burgrass (*Sparganium angustifolium*) at the east side near the outlet give the lake its name. Rush moor and heath moor, imperfectly developed in places, could not well be shown on the map.

Typical *sedge moor* has often been described (5, 7, 9). *Moss moor* and *true sedge moor* may be distinguished in the following quadrat records in which the percentage of ground covered by each kind of plant is indicated (tables 6 and 7). Naturally, any quadrat in a community would be different from every other quadrat as to minute details, but quadrat records afford the best means of distinguishing similar communities.

TABLE 6. *Meter quadrat in subalpine moss moor at Burgrass Lake (one of the Forest Lakes) in Gilpin County, Colorado, August 17, 1918. The figures indicate percentages of ground covered*

Bare ground	0
Mosses	40
Carex aquatilis	40
Clementsia rhodantha	5
Ligusticum tenuifolium	5
Caltha rotundifolia	5
Salix chlorophylla	2
Viola palustris	1
Epilobium anagallidifolium	1
Dodecatheon radicatum	1
	100

TABLE 7. *Meter quadrat in true subalpine sedge moor at Burgrass Lake (one of the Forest Lakes) in Gilpin County, Colorado, August 17, 1918. The figures indicate percentages of ground covered*

Bare ground	0
Carex aquatilis	60
Mosses	15
Carex nigricans and *C. illota*	5
Caltha rotundifolia	5
Elephantella groenlandica	5
Ligusticum tenuifolium	5
Salix spp.	4
Viola palustris	1
	100

Willow moor, or willow scrub, as previously suggested, is sedge moor with willows in it. The writer has usually thought of it as quite distinct from sedge moor, but on subalpine lake shores no sharp distinction can be drawn. It does not form, as a rule, a clearly marked circum-area, as is common in the montane region below 10,000 feet. Where present at subalpine lakes, willow moor is often a stage preceding the development of Engelmann spruce forest. This is especially true in late stages of infilling, when a whole lake may become willow moor and, later, spruce forest. Willows are most likely to develop on deep fine-grained soil. The species are *Salix chlorophylla, S. glaucops, S. lutea,* and *S. Barclayi.*

Rush moor is a society of sedge moor. On many shores it is very conspicuous as a narrow belt outside the ordinary sedge moor, most often when willows are absent. The usual species of rush are *Juncus Drummondii* and *J. mertensianus*, with, sometimes, *Juncoides spicatum.*

Meadow moor is sedge moor with some meadow plants. It may form a definite belt between moor and meadow, but more often it occurs as large or small patches developed on soil somewhat elevated above ordinary sedge moor and hence better drained. According to the writer's "soil moisture index" (6), ordinary xerophytes are given the number 4, mesophytes 6, marsh plants 8, and aquatics 10. Meadow moor would be assigned 7 as its index number. It is sometimes convenient to call it a "no. 7 meadow." There is less sedge and especially less moss than in ordinary sedge moor. More different species of plants occur than in ordinary sedge moor or in moss moor. The following are likely to be present in considerable amount: *Ligusticum tenuifolium, Erigeron salsuginosus, Bistorta bistortoides, Arnica fulgens* and *A. subplumosa, Deschampsia atropurpurea, Senecio blitoides.* Besides these, almost any of the true meadow plants may occur.

The *heath association* is here a mere suggestion of the heaths so prominent in the shore vegetation of many lakes in the northeastern United States and in Canada. The writer designates as "heath moor" the transition between moor and heath. This may be a distinct belt in which plants of the two associations are mingled, or it may be entirely lacking. In the latter case the belt of heath may follow abruptly after sedge moor or rush moor or meadow moor. It may be, in turn, followed on higher ground by forest, or there may be an intervening strip of meadow. Heath may occur in scattered patches on elevated areas of the sedge moor, probably most often in shallow soil over large rocks. A quadrat record (table 8) taken in a part of the heath which is not differentiated into consociations gives an idea of the floristic composition.

TABLE 8. *Meter quadrat in subalpine heath association at North Forest Lake (altitude 10,800 ft.) in Gilpin County, Colorado, August 17, 1918. The figures indicate percentages of ground covered*

Bare ground and rocks	20
Gaultheria humifusa	25
Vaccinium caespitosum	18
Kalmia microphylla	15
Erigeron salsuginosus	7
Carex festivella et spp.	5
Ligusticum tenuifolium	4
Juncus Drummondii	2
Agrostis humilis	2
Lichens	2
	100

The *Kalmia heath consociation* is characterized by the low shrub *Kalmia microphylla*, about 2 dm. tall. This is often only scantily distributed, but sometimes it forms a clearly-marked though narrow belt of vegetation part way around the moor. The writer has, in no case, seen a complete circum-area of this plant.

The *Gaultheria heath consociation* seems to develop often on shallow soil. In it dense patches of *Gaultheria humifusa* occur. The plant is a depressed undershrub only a few centimeters high. Subordinate species are *Vaccinium caespitosum*, *Muhlenbergia filiformis*, *Erigeron salsuginosus*, *Hieracium gracile*. Almost any meadow plant may occasionally be present.

The *meadow association* is conspicuous because of the large and brightly-colored flowers of some of the abundant species. It would be possible to name six or more societies of local or infrequent occurrence distinguished by floristic differences, but in the present paper it will be best merely to characterize two consociations. These, as already indicated in table 5, may be called the Erigeron-Castilleja-Ligusticum consociation and the Pedicularis-Vaccinium consociation. They are rather constant in occurrence, the first named being next to the heath (or to sedge moor or rush moor or meadow moor in some cases), the second merging into the undergrowth of the forest. There may be considerable bare ground (10 to 40 percent). Many species characteristic of lake-shore meadows in the montane zone (10, 11) are absent, as *Fragaria glauca*, *Tium alpinum*, *Potentilla pulcherrima*, *Erigeron macranthus*.

The *Erigeron-Castilleja-Ligusticum consociation* of the meadow develops on fine-grained soil with abundant moisture, and well drained. The dominant species are *Erigeron salsuginosus*, *Castilleja confusa* and *C. lauta*, and *Ligusticum tenuifolium*. Among other plants are *Potentilla diversifolia*, *Amarella strictiflora*, *Achillea lanulosa*, *Artemisia saxicola* and *A. scopulorum*, *Veronica Wormskjoldii*, *Phleum alpinum*, *Carex festivella*, *Bistorta bistortoides*, *Antennaria umbrinella*, and those mentioned in the following paragraph.

The *Pedicularis-Vaccinium consociation* is on drier ground than the community just described. *Pedicularis Parryi* and *P. Grayi* are important. *Vaccinium oreophilum*, a typical plant under Engelmann spruces, is usually present here at the edge of the forest. *Vaccinium scoparium* and *V. oreophilum* may also be present. All of these species of Vaccinium may at times be found sparingly in the Kalmia heath consociation. Many subordinate species of the Pedicularis-Vaccinium consociation are plants common in the forest or in forest openings, such as *Thlaspi Nuttallii*, *Chamaenerion spicatum*, *Koeleria gracilis*, *Micranthes rhomboidea*, *Aquilegia coerulea*. Then there are such meadow plants of the montane zone as *Dasystephana Parryi* and *Troximon glaucum*, and such plants of alpine meadow as *Trifolium dasyphyllum* and *T. nanum*. In addition there may be any of the species mentioned in the preceding paragraph.

TABLE 9. *Meter quadrat in subalpine meadow at Burgrass Lake (one of the Forest Lakes) in Gilpin County, Colorado, August 17, 1918. The figures indicate percentages of ground covered*

Bare ground and rocks	10
Ligusticum tenuifolium	12
Erigeron salsuginosus	8
Castilleja confusa	7
Castilleja lauta	7
Artemisia scopulorum and *A. saxicola*	6
Potentilla diversifolia	5
Arnica fulgens	5
Agrostis humilis	5
Mosses	5
Amarella plebeja	4
Veronica Wormskjoldii	4
Vaccinium caespitosum	4
Hieracium gracile	3
Viola bellidifolia	3
Phleum alpinum	3
Sibbaldia procumbens	3
Trifolium dasyphyllum	3
Chamaenerion spicatum	2
Juncus Drummondii	1
	100

An idea of the composition of the meadow may be gained from a quadrat record at Burgrass Lake. Where this was taken the belt of meadow was so narrow that the meter quadrat covered both consociations, and most of the common meadow plants are, therefore, represented. Ligusticum, it will be seen, occupied more space than any other species. Castilleja and Erigeron were, however, more conspicuous because of their brilliant flowers.

The *forest association* surrounding subalpine lakes does not differ from the forest elsewhere in the same locality. It is, therefore, not included in the present study.

List of Plant Species

The following list includes only the more frequent plants of subalpine lake shores. Certain species may be locally abundant and yet not widely distributed. These have generally been excluded. Plants belonging primarily to the forest and only occasionally getting in among the true moor, heath, and meadow plants are also not admitted, nor have aquatics been listed. A number of species characteristic of stream banks and of narrow gulches, as *Cardamine cordifolia, Heracleum lanatum, Primula Parryi, Mertensia ciliata,* and *Senecio triangularis,* are occasional in the moor but are not included in the list. Mosses, lichens, and fungi are not considered.

Many plants are lacking which are characteristic of lake shores at lower altitudes in Colorado and at ordinary altitudes in the United States east of the Rocky Mountains. The following may be mentioned: Equisetum, Typha, Alisma, Beckmannia, Panicularia, Cyperus, Scirpus, Iris, Populus, Betula, Persicaria, Rumex, Thalictrum, Rosa, Lathyrus, Vicia, Euphorbia, Menyanthes, Mentha, Prunella, Galium, Sambucus, Aster, Bidens, Iva, Rudbeckia, Solidago, Taraxacum. Some few of the above named are found in the shore vegetation of subalpine lakes close down to the 10,000-foot-altitude line, as Equisetum, Betula, Rosa. They do not, however, belong to typical subalpine lakes.

Since the soil moisture requirement is the most useful single feature to be known about a plant, provided the general climatic features of the region are known, this has been indicated in the list. The plan followed is that employed by the writer (6) and by one of his students (10) whereby, as previously stated, the figure 4 is used as the "soil moisture index" for ordinary xerophytes, 6 for mesophytes, 8 for marsh plants, 10 for aquatics. Most plants of sedge moor have a soil moisture index of 8, most plants of meadow have a soil moisture index of 6. Species which grow under various conditions are given more than one number.

Poaceae

Agrostis humilis (6, 7)
Alopecurus occidentalis (7, 8)
Deschampsia alpicola (6, 7, 8)
Deschampsia caespitosa (7, 8)
Koeleria gracilis (5, 6)
Muhlenbergia filiformis (6, 7)
Phippsia algida (7)
Phleum alpinum (7)
Poa alpina (7, 8)
Poa subpurpurea (5)
Sporobolus brevifolius (6)

CYPERACEAE

Carex albo-nigra (7, 8)
Carex aquatilis (8, 9)
Carex ebenea (7)
Carex festivella (6)
Carex nigricans (6, 7, 8)
Carex pyrenaica (6)
Carex rostrata (8, 9)
Carex scopulorum (8)

JUNCACEAE

Juncoides spicatum (5, 6, 7)
Juncus Drummondii (6, 7)
Juncus mertensianus (7, 8)

SALICACEAE

Salix Barclayi (8)
Salix chlorophylla (8, 9)
Salix glaucops (7, 8)
Salix lutea (8)

POLYGONACEAE

Bistorta bistortoides (7, 8)
Bistorta vivipara (7, 8)

ALSINACEAE

Alsine longifolia (7)

RANUNCULACEAE

Aquilegia coerulea (6)
Caltha rotundifolia (7, 8, 9)
Ranunculus alismaefolius (8)
Ranunculus alpeophilus (7, 8)
Trollius albiflorus

BRASSICACEAE

Draba Parryi (5, 6)
Thlaspi Nuttallii (5)

CRASSULACEAE

Clementsia rhodantha (8, 9)

SAXIFRAGACEAE

Micranthes arguta (8, 9)
Micranthes rhomboidea (6)

ROSACEAE

Dasiphora fruticosa (5, 6, 7)
Potentilla diversifolia (7)
Sibbaldia procumbens (6)

FABACEAE

Trifolium dasyphyllum (5, 6)
Trifolium nanum (5, 6)
Trifolium Parryi (5, 6)

VIOLACEAE

Viola bellidifolia (6)
Viola palustris (8)

ONAGRACEAE

Chamaenerion spicatum (5, 6)
Epilobium alpinum (8, 9)
Epilobium anagallidifolium (8, 9)
Epilobium Hornmannii (8)

AMMIACEAE

Angelica Grayi (8)
Ligusticum tenuifolium (7, 8)
Oxypolis Fendleri (7, 8)

ERICACEAE

Gaultheria humifusa (6, 7)
Kalmia microphylla (7)

VACCINIACEAE

Vaccinium caespitosum (5, 6)
Vaccinium oreophilum (5, 6)
Vaccinium scoparium (5, 6)

PRIMULACEAE

Androsace subumbellata (6)
Dodecatheon radicatum (8, 9)

GENTIANACEAE

Amarella monantha (8)
Amarella plebeja (7)
Amarella strictiflora (7, 8)
Chondrophylla Fremontii (8)
Dasystephana Parryi (6)
Dasystephana Romanzovii (6, 7)
Pleurogyne fontana (8)
Swertia scopulina (8, 9)

SCROPHULARIACEAE

Castilleja confusa (6)
Castilleja lauta (7)
Elephantella groenlandica (8)
Pedicularis Grayi (6)
Pedicularis Parryi (6, 7)
Pedicularis racemosa (5, 6)
Pentstemon stenosepalus (6)
Veronica Wörmskjoldii (8)

CAMPANULACEAE

Campanula petiolata (5, 6, 7)

CARDUACEAE

Achillea lanulosa (5, 6, 7)
Antennaria umbrinella (6)
Arnica fulgens (6)
Arnica Parryi (6)
Arnica subplumosa (6)
Artemisia saxicola (6)
Artemisia scopulorum (6)
Erigeron salsuginosus (6, 7)
Oreochrysum Parryi (5, 6)
Senecio blitoides (6)
Senecio crassulus (6, 7)

CICHORIACEAE

Agoseris glauca (5, 6)
Hieracium gracile (6)

SEASONAL ASPECTS

The growing period of subalpine lake-shore vegetation may be separated (9) into three seasons: vernal (May 15 to July 1), estival (July 1 to August 15), autumnal (August 15 to October 1).

During the vernal period there are few lake-shore plants in bloom. About June 1 or a little later the willow catkins appear. The brown of winter continues, especially at higher altitudes, until the middle of June. There are still large snowdrifts in the forest and often some in the open. It must not be thought that there is no fresh vegetation in the subalpine zone at this time. A number of xerophytic plants of ridges and dry slopes and forest openings are in bloom, but these do not belong to our present study. Of lake-shore plants, in addition to the willows already mentioned, the spring bloomers are Caltha, Trollius, *Viola bellidifolia*, *V. palustris*, *Thlaspi Nuttallii*, *Draba Parryi*. Caltha and Trollius, on account of their abundance and their showy flowers, are the conspicuous plants of the spring season.

During the estival period the great majority of lake-shore plants come into blossom. Many of the sedges are rather early; grasses are somewhat later. The spring flowers continue for a time but are soon overshadowed by the abundance and brilliancy of the summer bloomers. In the moor there are Clementsia, Dodecatheon, Elephantella, Dasiphora, Swertia, and Senecio. Among meadow and heath plants may be mentioned the Castillejas, the Arnicas, *Potentilla diversifolia*, Kalmia, Campanula, *Erigeron salsuginosus*, *Hieracium gracile*.

During the autumnal period the summer-blooming plants are in fruit and a few of them continue to bloom for a time, especially *Erigeron salsuginosus*, *Campanula petiolata*, the Castillejas, and the Arnicas. True autumn-blooming plants are the gentians Amarella, Chondrophylla, and Dasystephana, also *Antennaria umbrinella* and *Ligusticum tenuifolium*. The snows which usually come about the first week in September melt away in a few days, and some of the plants continue in bloom up to about September 20, or occasionally even to October 1.

Successions

The character of succession on the lake shores here described is so obvious that an extended discussion will not be necessary. It needs to be kept in mind that the topography of the area is "new." There is comparatively little soil anywhere except in depressions where it has been washed down from adjacent slopes. Lake bottoms are typically of boulders. Climate is of the cold, moderately wet type which favors the development of coniferous forest. Engelmann spruce forest is the ultimate climatic association and appears wherever edaphic conditions are at all favorable.

A few subalpine lakes, especially those at lower altitudes close to 10,000 feet, have a moderate amount of aquatic vegetation, chiefly *Potamogeton* spp. and *Sparganium angustifolium*. These plants contribute slightly to the filling up of lakes. At higher altitudes they are generally absent and the only lake vegetation of consequence is Carex, which may form in places a strip of half submersed plants extending into the water from the moor. The Carex here is commonly *C. aquatilis*, which is also the chief sedge of the moor that surrounds subalpine lakes.

Often the vegetation advances very slowly into the lake because of the heaving action of ice. This thrusts itself into the bank and destroys vegetation. It may give rise to an elevated "rim" as shown by Robbins (11), projecting out a few decimeters over the edge of the water.

Infilling of subalpine lakes is, it will be recognized, largely a physiographic process depending upon stream sediment chiefly near the inlet, or upon storm wash from surrounding slopes. When, however, a lake has once been filled so that the water is quite shallow, then a rapid invasion by Carex may occur.

The normal positions of the various plant communities show their successional relations. Half submersed Carex association is followed by moor, and this by heath and meadow and forest. When level ground is raised by accumulation of plant remains or by alluvial wash then a later successional stage of vegetation develops. The same change occurs when the lake level is lowered. One or more stages may be skipped.

Moss moor is usually the wettest part of the moor. As vegetation advances this becomes drier and changes to ordinary sedge moor or to meadow moor. The willow moor stage may follow sedge moor if there is a good depth of fine-grained soil. While in montane situations willows tend to form a complete circum-area of lakes, they are relatively unimportant in the shore vegetation of the subalpine region. Where they do occur they may initiate a shortened successional series, for they permit the establishment of Engelmann spruce without the intermediate heath and meadow stages.

"Dry forest" of limber pine and lodgepole pine does not follow meadow but belongs to the xerarch series, developing on ridges and on rough, stony ground. In time, except where winds are so severe as to blow away the humus, Engelmann spruce forest, as the ultimate climatic association, will replace the dry forest.

SUMMARY

The subalpine zone, 10,000 to 11,500 feet in altitude, in north-central Colorado has a large number of small lakes, some of morainal, some of rock-basin type. These have a characteristic shore vegetation often developing definite circum-areas. The climatic climax association is Engelmann spruce forest, and the stages of succession in the filling up of a lake lead eventually to this forest. Very few aquatic plants occur, but there is sometimes a circum-area (usually incomplete) of half submersed sedges. Following this there may be in the more complete cases: (1) a well developed moor composed largely of Carex, sometimes separable into moss moor, sedge moor, willow moor, rush moor, and meadow moor; (2) a heath association of *Kalmia microphylla* and *Gaultheria humifusa;* (3) meadow association in which the principal plants are species of Erigeron, Castilleja, Ligusticum, Pedicularis, and Vaccinium; (4) forest association, dominated by Engelmann spruce. The various associations and their numerous subdivisions are described by the author together with their successional relations and seasonal aspects. A sketch is given of topography, climate, and soil, and a list is made of the characteristic lake-shore plants, with soil-moisture index of each. The paper is based upon the study of a large number of subalpine lakes in four different counties of north-central Colorado.

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